

Patterns and traits associated with invasions by predatory marine crabs

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Abstract

Predatory crabs are considered amongst the most successful marine invasive groups. Nonetheless, most studies of these taxa have been descriptive in nature, biased towards specific species or regions and have seldom considered traits associated with invasiveness. To address this gap in knowledge, this study presents a global review of invasions by this group and applies biological trait analysis to investigate traits associated with invasion success. A total of 56 species belonging to 15 families were identified as having spread outside their native ranges. The family Portunidae supported the highest number of alien species (22). Most crabs had their origin in the North West Pacific IUCN bioregion while the Mediterranean Sea received the most species. No traits associated with successful establishment were identified, but this finding may reflect the paucity of basic biological knowledge held for many species. This lack of foundational knowledge was unexpected as crabs are large and conspicuous and likely to be well studied when compared to many other groups. Addressing this knowledge gap will be the first step towards enabling approaches like biological trait analysis that offer a means to investigate generalities in invasions.

Keywords

Biological invasions, establishment success, shipping, trait analysis

Introduction

Studies reviewing the distribution and vectors of marine alien species are numerous and include those that focus at the global (e.g. Bax et al. 2003, Ruiz et al. 2011) and regional scale (e.g. Europe (Galil et al. 2014); South Africa (Mead et al. 2011)). However, these studies are often descriptive in nature, providing first insights into the marine invasions of a region. Recently, there has been a move to advance this approach by identifying invasion patterns and applying biological trait analysis to identify taxa that are likely to invade. The use of these approaches adds statistical power to the conclusions drawn about the factors that may play a role in the spread and establishment of alien species (Cardeccia et al. 2018). An additional approach to understanding patterns of invasions comes in the form of taxon-specific reviews (e.g. Novoa et al. 2015, Marchini and Cardeccia 2017). Such reviews can be insightful as they focus on highly invasive taxa from well-studied groups, enabling detailed analyses of factors driving their invasion success (Kolar and Lodge 2002, Hänfling et al. 2011).

Brachyuran crabs that spend all or part of their life-cycle in the marine environment (hereafter collectively referred to as marine crabs) are a globally successful invasive group (Brockerhoff and McLay 2011), associated with significant ecological (Kraemer et al. 2007, Garbary et al. 2014) and socio-economic impacts (White et al. 2000, Chakraborty et al. 2002). This success likely reflects the diverse nature of this group, which is known for broad salinity and temperature tolerances (Dittel and Epifanio 2009), good dispersal abilities (Gust and Inglis 2006) and high reproductive potential (Brousseau and McSweeney 2016). In light of the large invasive ranges and notable impacts associated with some crab species (e.g. *Hemigrapsus sanguineus* (Kraemer et al. 2007); *Charybdis hellerii* (Felder et al. 2009) and *Carcinus maenas* (de Rivera et al. 2011)), crab invasions have received considerable attention in the literature. However, studies considering these invasions have been mostly region specific (e.g. Mediterranean (García Muñoz et al. 2008)) or species specific (e.g. *Eriocheir sinensis* (Veilleux and de Lafontaine 2007)). While some species-specific studies have considered traits, they have generally applied one of two approaches: comparing the traits of alien species in their native and invaded ranges (Grosholz and Ruiz 2003) or comparing traits between an established alien species and native species in a particular region (Brousseau and McSweeney 2016). These studies were, however, biased towards well known species and have considered only a few select traits and, thus, do not reveal general patterns about the invasiveness of marine crabs as a group. While there has been one review of crab invasions (Brockerhoff and McLay 2011), this study was broad in its taxonomic focus (i.e. it considered brachyuran crabs as well as two families from the crab-like anomurans). The application of a multi-species, multi-trait approach to identify trait profiles associated with the successful invasion of crabs is thus lacking.

In an effort to address this gap, we used predatory brachyuran crabs (i.e. those that kill prey for food) as a case study. This study reviewed invasions within this functional group. This study aimed to 1) compile a list of marine predatory crabs with an invasion history; 2) document their donor and receiving bioregions and

3) consider traits that may be associated with their successful establishment. Based on literature (Weis 2010, Hänfling et al. 2011), it was hypothesised that traits that predispose species to being able to survive under a variety of conditions (e.g. broad habitat requirements) would typify crab species that have established alien populations. In contrast, traits that facilitate transfer by humans (e.g. long larval development) would be shared by both established species and those that are represented by only single records outside of their native ranges. Identifying traits that are important in the invasion process will help to further our understanding of which species are predisposed to becoming successful invaders.

Methods

Species and variables reviewed

To compile a list of predatory crabs with an invasion history, we reviewed the literature reporting on marine crab invasions across the globe. Information regarding each species in both their native and alien ranges was recorded (Table 1). Brachyuran crabs were included if they met the following inclusion criteria: (1) they could be classified as alien following Robinson et al. (2016); (2) they were fully marine or catadromous; (3) they were predatory in nature (i.e. they kill live prey) and (4) their native ranges could be defined. A total of 39 species were excluded based on these criteria (see Suppl. material 1 for a full species list and the exclusion criteria applied to each). Species were classified to family level following the World Registry of Marine Species (WoRMS).

The list of alien species was established using scientific literature and a variety of online databases including WRIMS: World Register of Introduced Marine Species (<http://www.marinespecies.org/introduced/>), CABI: Centre for Agriculture and Biosciences International (<http://www.cabi.org/isc/>), GISD: Global Invasive Species Database (<http://www.iucngisd.org/gisd/>) and CIESM: The Mediterranean Science Commission Atlas of exotic crustaceans in the Mediterranean (<http://www.ciesm.org/atlas/index.html>). Smaller regional databases were used when appropriate. Additional sources of information used included published books, technical reports and online theses, all sourced using Google Scholar (see Suppl. material 2 for a complete list of sources). Compilation of the species list was undertaken between September and November 2015, while the extraction of relevant information was carried out between November 2015 and February 2016.

It has been suggested that the most appropriate method for characterising traits of invasive species is to compare invaders with those of the same taxonomic group that have not spread outside their native ranges (Nawrot et al. 2015, Novoa et al. 2015). While the strengths of this approach are clear, it was not viable to do so for crabs. This was because this group is large (containing 1271 genera and an estimated 6793 described species (Ng et al. 2008)) and widely distributed, occurring on all continents. In addition, trait information is simply not available for most species. While this

Table 1. Information that was recorded for each predatory crab in their native and alien ranges.

Variables	Data recorded
Invasion status	Species reported only from a single record or established populations.
Distribution range	Using reports in the literature, species ranges were defined in terms of provinces (as defined by Spalding et al. (2007)). If a species had been reported from a location within a province, its distribution was taken to include that whole province.
Donating and receiving regions	These regions were defined following the IUCN bioregions defined by Kelleher et al. (1995a, b, c, d).
Biological traits	Size, adult longevity, adult mobility, fecundity, migratory behaviour, larval development time, generation time (See Table 2 for details).
Ecological traits	Range size, substratum type (See Table 2 for details).

approach was pursued using species from a well-studied region (i.e. China using the Chinese Registry of Marine Species; ChaRMS), trait information was available for less than 3% of crab species, resulting in the abandonment of this methodology. As a result, to get a better understanding of the patterns of crab invasions and the traits that may play a role in invasion success, we compared those alien species that have been documented as supporting established populations with those species for which no evidence exists for their successful establishment. Single record species were defined as those with single or sporadic recordings, in contrast to established species that were defined as those with self-sustaining populations. To assess if the number of established species is related to the number of alien species known from a family, a Spearman’s rank correlation was undertaken. All univariate analyses were done in Statistica (version 13) unless otherwise stated.

Distribution ranges

Native and invaded range sizes were determined for each species. Range size was defined as the number of marine provinces (as defined by Spalding et al. 2007) in which a species occurred. The relationship between native and invaded range was investigated using a Spearman’s rank correlation.

Donating and recipient regions

Determining the origin of introductions can be challenging. While the origin of species can be confirmed through the use of genetic techniques, in the absence of such studies, two pragmatic approaches can be applied. The first, considering the whole native range as a potential source, is the most conservative approach. The second, deducing origins using the most likely shipping routes (Seebens et al. 2013), is founded on the assumption that most marine alien species are introduced via shipping, an assumption that can introduce error. This process has seldom been undertaken with respect

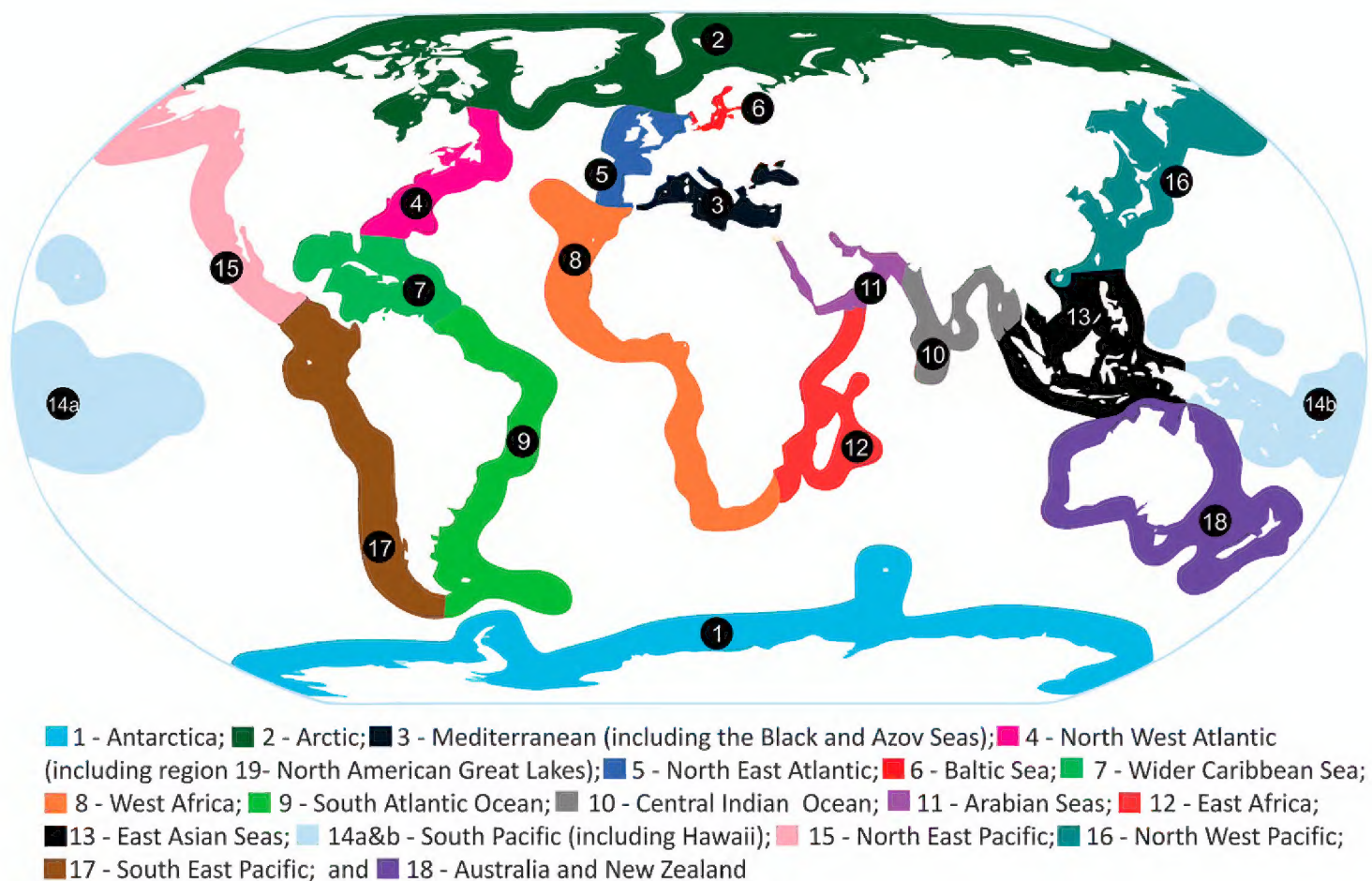


Figure 1. Map illustrating the 18 IUCN bioregions. The 18 IUCN bioregions used for identifying the donating and receiving regions of crab invasions. Bioregions defined by Kelleher et al. (1995a, b, c, d). Figure modified from Hewitt et al. (2011).

to crab introductions. As such, in this study, both approaches were applied if a species origin was not explicitly given in the literature. This enabled the two approaches to be contrasted. Potential donating and receiving regions were defined in terms of the 18 IUCN bioregions (Kelleher et al. 1995a, b, c, d; Figure 1). The package *circulize* in R (version 3.3.2) was used to visualise the relationships between the various regions through the use of a chord diagram.

Analysis of traits

Detailed information on the biological and ecological traits (hereafter referred to as traits) of each species were recorded and categorised. Each trait had a minimum of two and maximum of four categories (Table 2). Nine of the traits suggested to be important in contributing to invasion success were included (Crawley 1989, Ehrlich 1989, Weis 2010, Hänfling et al. 2011) (Table 2). While it would have been preferable to include salinity and temperature tolerance and growth rate, these had to be excluded due to a lack of information in the literature. Definition of traits and categories were adapted from Bremner et al. (2006), MarLIN (2006) and Cardeccia et al. (2018).

The affinity of each species to the trait categories was captured by allocating a score from 0–4 to each category of every trait, where 0 reflects no affinity and 4 a high affinity. As the “fuzzy coding” approach (Chevenet et al. 1994) was applied, a

Table 2. Trait information that was recorded for each alien species.

Traits	Information recorded	Categories
Size	Maximum carapace width (cm)	Small (≤ 5), Medium (5.1–10), Large (10.1–15), X-large (≥ 15.1)
Longevity	Maximum age (years)	Short (≤ 2), Medium (3–5), Long (6–8), Very long (≥ 9)
Adult mobility	Mode of movement and behaviour	Walking, Swimming, Burrowing, Drifting
Migratory behaviour	Migratory or not	Seasonal migration, Non-migratory
Larval development time	Development time (days)	Short (≤ 20), Long (21–40), Protracted (≥ 41)
Fecundity	Number of eggs/year	Low (≤ 0.25 mil), Medium (0.25–0.5 mil), High (0.5–2 mil), Very High (≥ 2 mil)
Generation time	Average time between two consecutive generations (months)	Short (≤ 12), Medium (13–23), Long (≥ 24)
Range size	Number of provinces (Spalding et al. 2007)	Small (1), Medium (2–5), Large (6–10), Very Large (≥ 11)
Substratum type	Types of substratum in which species are present	Sandy (sandy/ muddy/ saltmarsh/ seagrass/ eelgrass/ clay), Rocky (rocky/ oyster beds/ algae/ seaweed), Artificial, Biogenic reefs (syllid tubes/ coral)

species could receive several scores for any trait, thus incorporating variation in the affinity of a species to trait categories. For each trait, the sum of the scores for the various categories added up to 4. This allowed the transformation of trait data into quantitative affinity values that could be used in multivariate analysis. To attribute affinities consistently across traits, set criteria were applied. When a species showed an affinity for multiple categories, the category most frequently displayed received the highest score while, if two categories were equally represented, an affinity of 2 was allocated for both. For example, the habitat generalist *Carcinus maenas* was assigned an affinity of 1 for all substratum types, *Charybdis japonica* was assigned an affinity of 2 for both sandy and rocky substrata but zero for biogenic reefs and artificial habitats as it has not been reported from these substrata, while the sandy shore specialist *Scylla serrata* was allocated an affinity of 4 for sandy habitats. When literature detailing traits was contradictory, scores were assigned based on expert judgement. Information was obtained at the species level, but in the event that information was not available at this level, a search was conducted at the genus level. Following Fledum et al. (2013), if information was still unavailable, a zero was allocated to all categories within that trait. When information was not available for three or more traits for any species, it was excluded from the analysis. Traits were thus analysed for 28 species (Table 3). Please see Suppl. material 3 for full details of the trait affinities of each species. To identify if certain suites of traits predispose species to successfully establishing alien populations, the traits of single record species were compared to those of established species.

Table 3. List of 56 alien crab species from 15 families. Labels apply to Figure 5. (*) denotes single record species. (#) indicates the 28 species that were included in the trait analysis.

Taxa	Labels	Taxa	Labels
Calappidae		Portunidae	
<i>Calappa hepatica</i>	<i>CalH</i>	<i>Callinectes bocourti</i>	<i>CalB</i>
		<i>Callinectes danae</i> **	<i>CalD</i>
Cancridae		<i>Callinectes exasperatus</i> **	<i>CalE</i>
<i>Cancer irroratus</i> #	<i>CanI</i>	<i>Callinectes sapidus</i> #	<i>CalS</i>
<i>Glebocarcinus amphioetus</i> #	<i>GleA</i>	<i>Carcinus aestuarii</i> #	<i>CarA</i>
<i>Metacarcinus magister</i> **	<i>MetM</i>	<i>Carcinus maenas</i> #	<i>CarM</i>
<i>Metacarcinus novaezelandiae</i> #	<i>MetN</i>	<i>Carupa tenuipes</i>	<i>CarT</i>
<i>Romaleon gibbosulum</i>	<i>RomG</i>	<i>Charybdis feriata</i> **	<i>ChaF</i>
		<i>Charybdis hellerii</i> #	<i>ChaH</i>
Carpiliidae		<i>Charybdis japonica</i> #	<i>ChaJ</i>
<i>Dyspanopeus sayi</i> #	<i>DysS</i>	<i>Charybdis longicollis</i>	<i>ChaLo</i>
		<i>Charybdis lucifera</i> *	<i>ChaL</i>
Dairidae		<i>Charybdis variegata</i> *	<i>ChaV</i>
<i>Daira perlata</i> *	<i>DaiP</i>	<i>Gonioinfradens paucidentatus</i>	<i>GonP</i>
		<i>Liocarcinus navigator</i> **	<i>LioN</i>
Grapsidae		<i>Necora puber</i> #	<i>NecP</i>
<i>Metopograpsus oceanicus</i>	<i>MetO</i>	<i>Portunus pelagicus</i> #	<i>PorP</i>
<i>Pachygrapsus marmoratus</i> #	<i>PacM</i>	<i>Portunus segnis</i> #	<i>PorS</i>
<i>Pachygrapsus transversus</i> #	<i>PacT</i>	<i>Scylla serrata</i> #	<i>ScyS</i>
<i>Percnon gibbesi</i> #	<i>PerG</i>	<i>Thalamita gloriensis</i>	<i>ThaG</i>
		<i>Thalamita indistincta</i>	<i>ThaI</i>
Hymenosomatidae		<i>Thalamita poissonii</i>	<i>ThaP</i>
<i>Elamena mathoei</i> *	<i>ElaM</i>		
<i>Haliscarcinus innominatus</i>	<i>HalI</i>	Raninidae	
<i>Haliscarcinus planatus</i> **	<i>HalP</i>	<i>Notopus dorsipes</i> *	<i>NotD</i>
Matutidae		Varunidae	
<i>Ashtoret lunaris</i> *	<i>AshL</i>	<i>Brachynotus sexdentatus</i> *	<i>BraS</i>
<i>Matuta victor</i> *	<i>MatV</i>	<i>Eriocheir hepuensis</i> #	<i>EriH</i>
		<i>Eriocheir japonica</i> **	<i>EriJ</i>
Menippidae		<i>Eriocheir sinensis</i> #	<i>EriS</i>
<i>Sphaerozium nitidus</i> *	<i>SphN</i>	<i>Hemigrapsus sanguineus</i> #	<i>HemS</i>
		<i>Hemigrapsus takanoi</i> #	<i>HemT</i>
Oregoniidae			
<i>Chionoecetes opilio</i> #	<i>ChiO</i>	Xanthidae	
		<i>Atergatis roseus</i>	<i>AteR</i>
Panopeidae		<i>Xanthias lamarckii</i> *	<i>XanL</i>
<i>Panopeus lacustris</i>	<i>PanL</i>		
Pilumnidae			
<i>Actumnus globulus</i> *	<i>ActG</i>		
<i>Eurycarcinus integrifrons</i>	<i>EurI</i>		
<i>Pilumnopus vauquelini</i>	<i>PilV</i>		
<i>Pilumnus minutus</i> *	<i>PilM</i>		
<i>Pilumnus spinifer</i> *	<i>PilS</i>		

A combination of multivariate methods was used to analyse traits. This allowed the identification of patterns in the trait profiles of a cluster of species (Bremner et al. 2006). A hierarchical cluster analysis was performed on the matrix of species by trait categories and used to identify clusters of species sharing similar suites of traits (i.e. groups displaying corresponding trait affinities), ecological equivalents (i.e. species sharing exactly the same traits) and outliers (i.e. species displaying a unique combination of traits). This analysis enabled the measurement of the level of similarity of the trait profiles amongst the alien crab species and the consideration of differences between established and single record species (Cardeccia et al. in press). Analyses were performed in PRIMER (version 6) and applied to fourth-root transformed non-standardised data, based on Bray-Curtis similarities.

As cluster analysis is unable to identify the traits responsible for the variation observed, Fuzzy Correspondence Analysis (FCA) was performed on the data matrix to explore this feature. This multivariate analysis is adapted to analyse fuzzy coded data and applies Euclidean distances that are calculated from the frequencies of each trait category to ordinate the species (Chevenet et al. 1994; Bremner et al. 2006). The plot, generated by the FCA, was used to identify patterns in the trait profiles of species and identify the traits responsible for the variation in the data. The traits of a species determines its distribution across the plot, with species sharing similar traits located close to each other. To enable consideration of status (i.e. single record or established species) and family in relation to species that share similar traits, species were labelled according to these variables on the FCA plots. These analyses were conducted in R (R Core Team 2018) using the library *ade4*. Traits were also considered separately to identify those traits that varied most amongst species. The correlation ratio between each trait and the FCA axes was calculated. The higher the correlation ratio, the more that trait accounts for variation within the data.

Results

A total of 56 alien predatory brachyuran crab species from 15 families were identified as having spread outside of their native ranges (Table 3). The highest number of alien species (22) was supported by the family Portunidae (i.e. the swimming and shore crabs). Of the 56 alien species, 36 (64%) had been reported as supporting established populations (Figure 2). In contrast, 20 were classified as single record species (supporting information is presented in Suppl. material 4). The largest number of established species was from the family Portunidae and included species such as the European shore crab, *Carcinus maenas*. Other families supporting notable numbers of established alien species were the Varunidae (i.e. mitten crabs), Cancridae (i.e. rock crabs), Pilumnidae (i.e. hairy crabs) and Grapsidae (i.e. marsh crabs), highlighting a positive correlation between the number of alien species known from a family and the number of established species in that family (Spearman's rank correlation; $r = 0.79$, $p < 0.001$). Notably no such relationship was found between the number of established species within a family and the total number of species known from the family (Spearman's rank correlation; $r = 0.50$; $p = 0.057$).

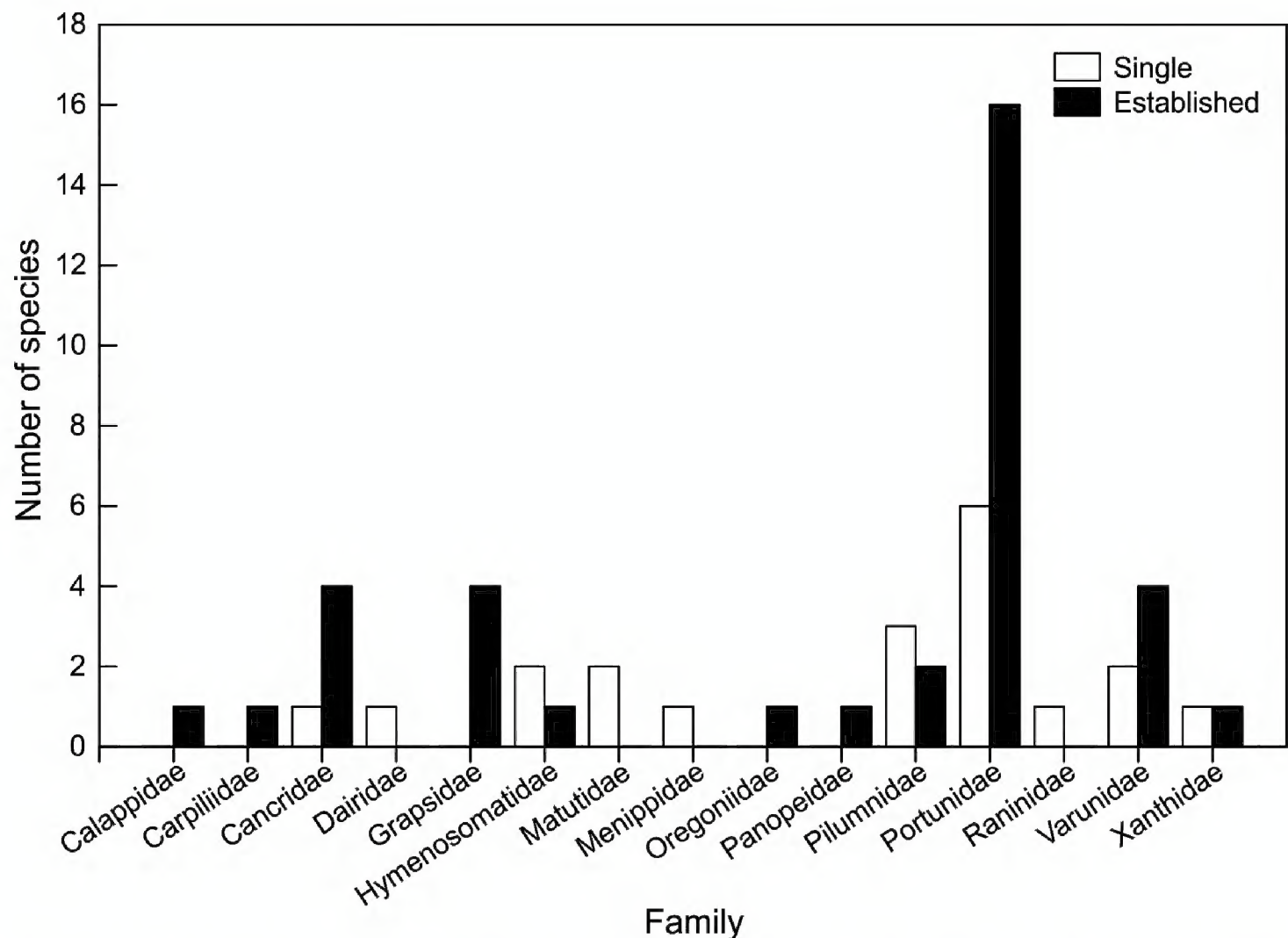


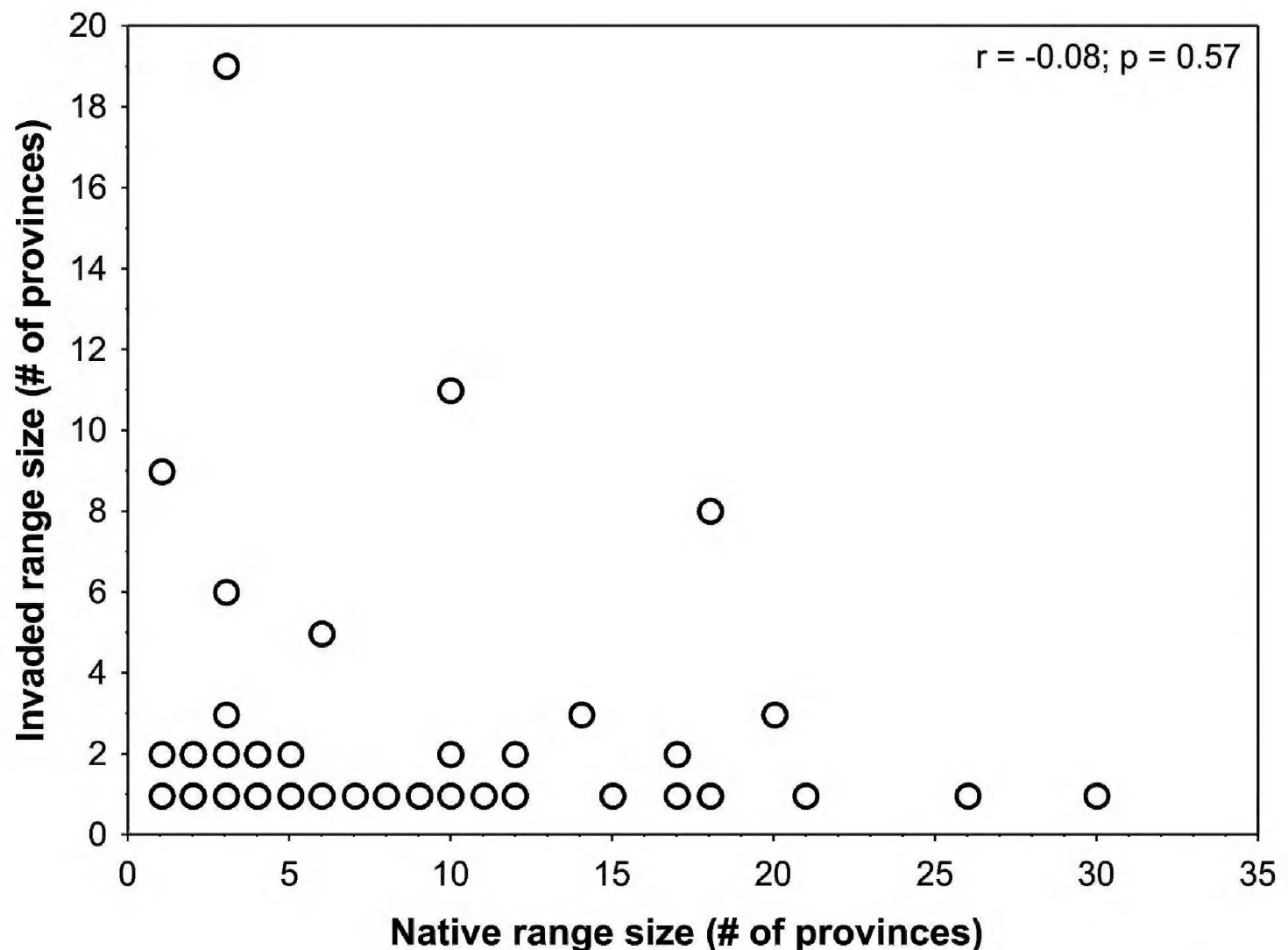
Figure 2. Number of established and single record predatory alien crab species recorded in each family.

Distribution ranges

Only 15 species had very large native ranges (≥ 11 provinces) and it was notable that the invaded ranges of these crabs were amongst the smallest ($\leq$ three provinces) with the exception of one species, the Indo-Pacific swimming crab, *Charybdis hellerii*, that had an invaded range size of eight provinces (Figure 3). Notably, no correlation was found between native and invaded range sizes of alien crabs (Spearman's rank correlation; $r = -0.08$, $p = 0.57$).

Potential donating and recipient regions

When considering native bioregions as the potential source for each alien crab introduction, it was found that all 18 IUCN bioregions have potentially acted as source regions (Figure 4a). This is in contrast to 15 bioregions that were identified when shipping routes were used to deduce source regions (Figure 4b). The Mediterranean Sea was the most invaded bioregion, receiving 33 species. Notably, the Arabian Seas were the source of most of these introductions when using shipping connectivity to identify donor regions. However, because of the large native range of many of these species, they could in fact have been introduced from any of 11 bioregions including the South Pacific, East Asian



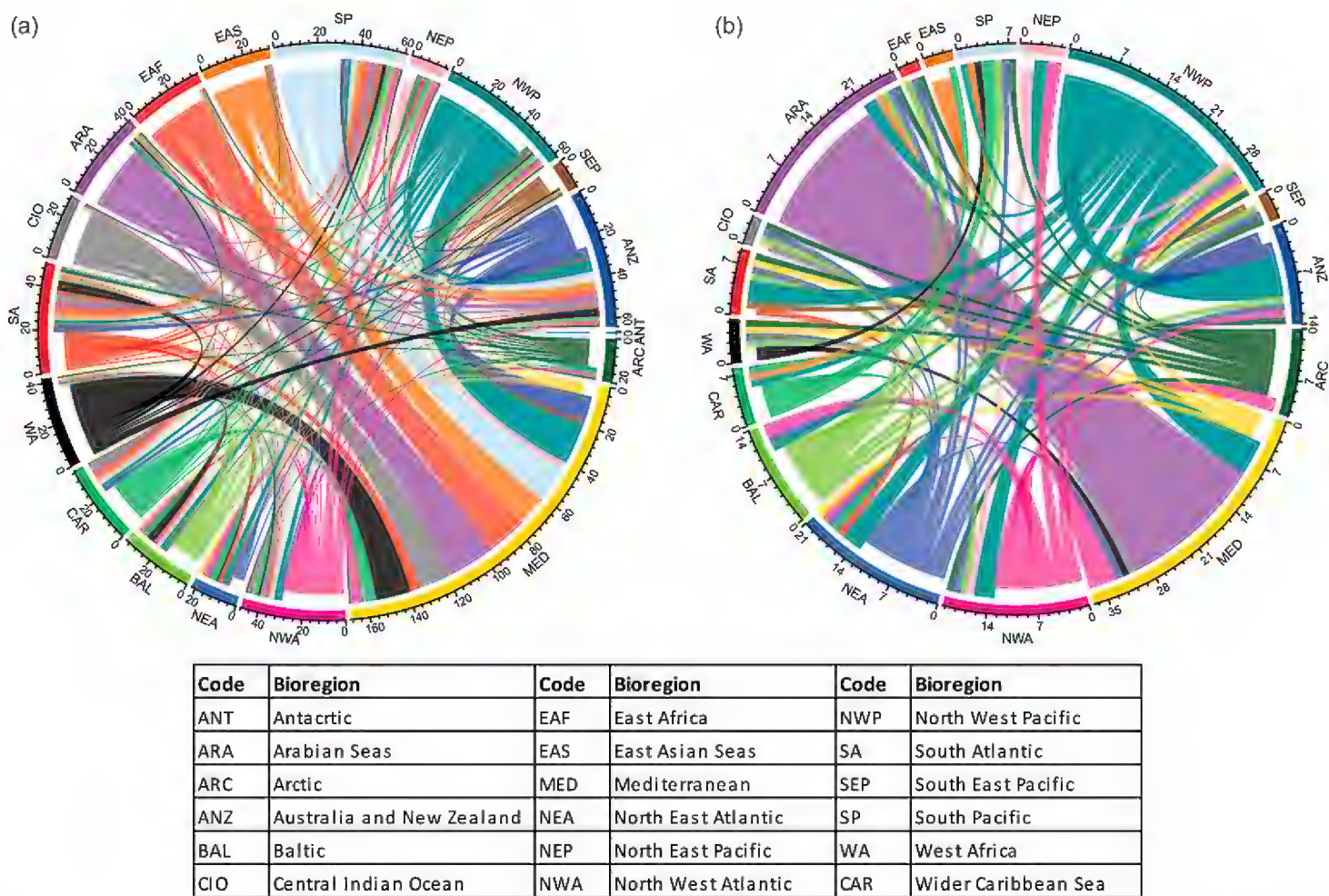


Figure 4. Bioregions that receive and potentially donate alien crab species. Where donating regions were not confirmed in the literature, they were determined using (a) the native range of the alien crabs and (b) using the most likely shipping routes (Seebens et al. 2013). Bioregions are represented by the different coloured segments. Lines that are the same colour as the segments represent species donated from that bioregion. Lines radiate to the bioregions to which species were donated. The numbers around the diagram represent the numbers of species (both native and alien) in each bioregion.

variability within the dataset, with the first axis explaining the most variability. For this dataset, very little of the total variability was explained by trait similarity (Axis 1 + Axis 2 = 31%; Figure 6). To investigate if any patterns in the traits displayed by the crabs were related to their invasion status or family, these variables were overlaid on Figure 6. Unexpectedly, species did not form separate groups based on either of these variables, rather they were interspersed across the plot indicating that separate suites of traits are not associated with the different status levels or families. To fully interpret the FCA results, Figure 6 should be considered along with Figure 7. Each block in Figure 7 represents one of the nine traits considered and the stars represent the distribution of the different categories within that single trait. The centre of each star corresponds to the centre of gravity of all the species that display that trait category and the rays link the species to their categories. While some traits, such as migratory behaviour and carapace size, explained variability in the data (i.e. they separate out along the two axes), most traits showed little separation amongst categories (e.g. substratum type).

Together with the correlation ratios (Table 4), Figure 7 was used to identify the most important traits driving the variation observed in Figure 6. High correlation

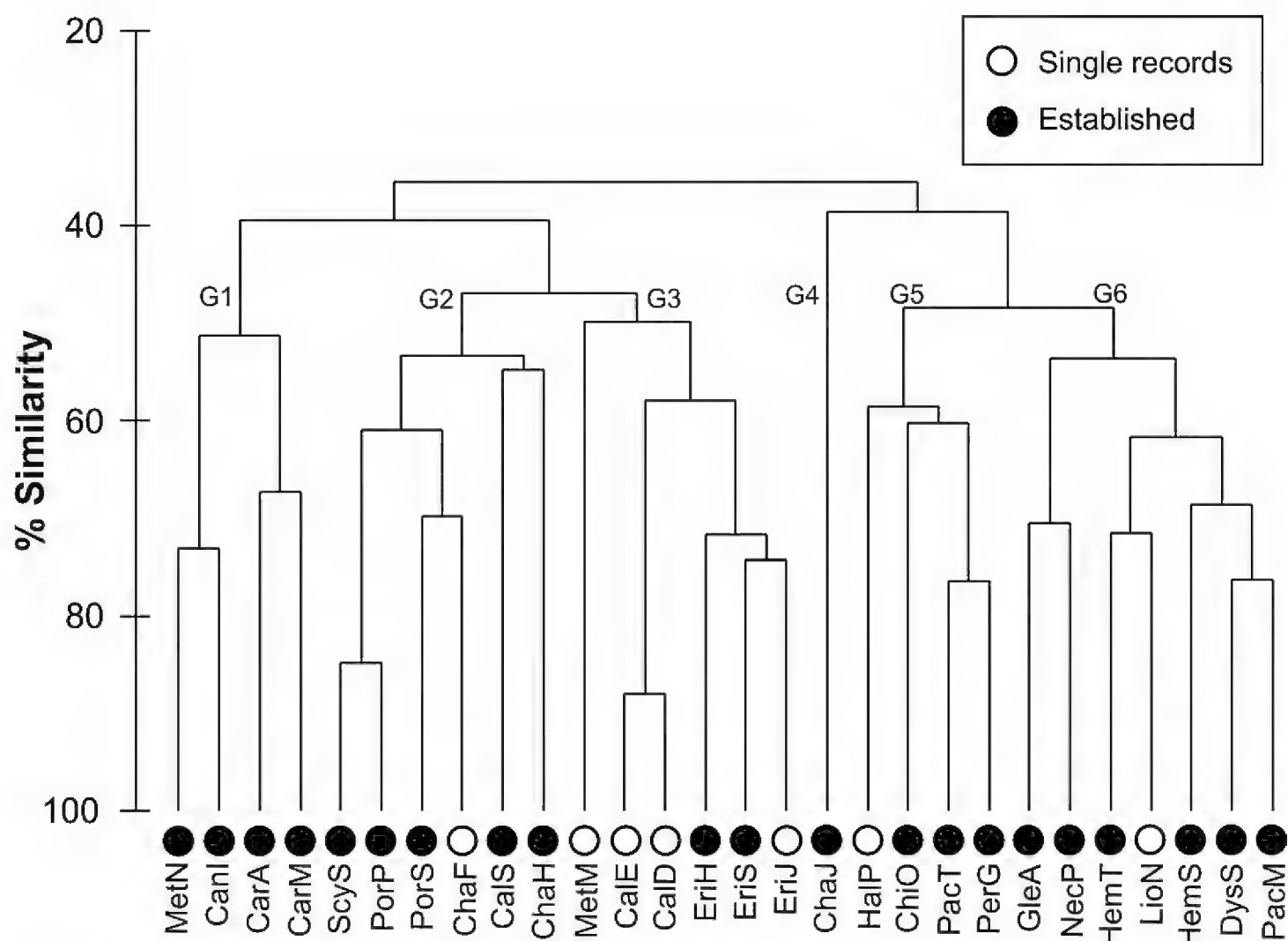


Figure 5. Dendrogram based on Bray-Curtis measures of similarity for single record and established species. The 6 groups of species identified at the 50% similarity threshold are indicated by G1–G6. See Table 3 for species labels.

values identify traits that explain high levels of variability in the data and are reflected in Figure 7 as traits that have stars that separate out along the two axes. Carapace size was identified as being responsible for the most variation along the axes as it has the largest correlation ratios for both axes (Table 4). This is demonstrated by the categories separating out on both axes (Figure 7). Other important traits accounting for variation along the axes included fecundity (for both axes), migration for Axis 1 and longevity, generation time and range size for Axis 2. In contrast, some categories (e.g. substratum type) did not separate out across the axes, but rather clustered at the origin, indicating that these traits did not vary amongst species.

Discussion

Due to the prevalence of, and threats posed by, alien species (Simberloff et al. 2013), there is great value in understanding generalities governing invasions. Predatory crabs are amongst the most successful marine invasive taxa (Brockerhoff and McLay 2011, Brousseau and McSweeney 2016). To better understand the complex drivers and traits behind this success, we reviewed all invasions within this functional group and compiled a list of 56 alien marine predatory crab species from 15 families. Most alien

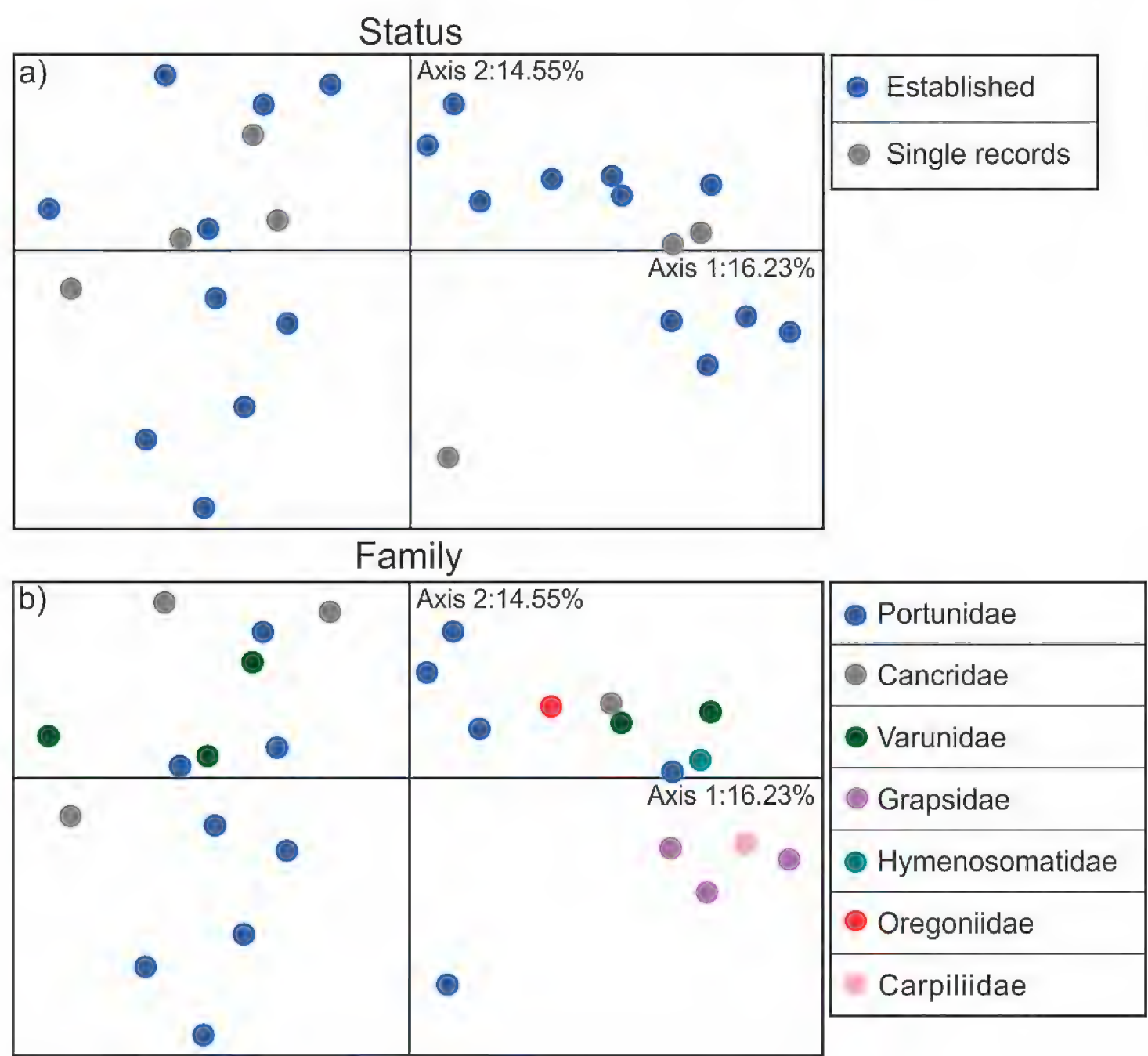


Figure 6. Fuzzy Correspondence Analysis (FCA) bidimensional plot where every dot represents one of the 28 alien crab species. Species are labelled according to status [in **a)**] and family [in **b)**].

crabs originated in the North West Pacific, while the Mediterranean Sea was the most invaded bioregion. Unexpectedly, it was found that neither ecological nor biological traits were good predictors of establishment success.

Patterns observed in crab invasions

Similarly to the findings of Brockerhoff and McLay (2011), the family from which the greatest number of alien brachyuran crab species was noted, was the Portunidae. It is notable that, despite supporting the highest number of alien and established species, the Portunidae are not the largest family of brachyuran crabs. The most speciose family is the Xanthidae, which supports more than double the number of species than the Portunidae, but has only two species known to be alien. While this may suggest that the Portunidae possess traits that predispose them to being successful invaders, this was

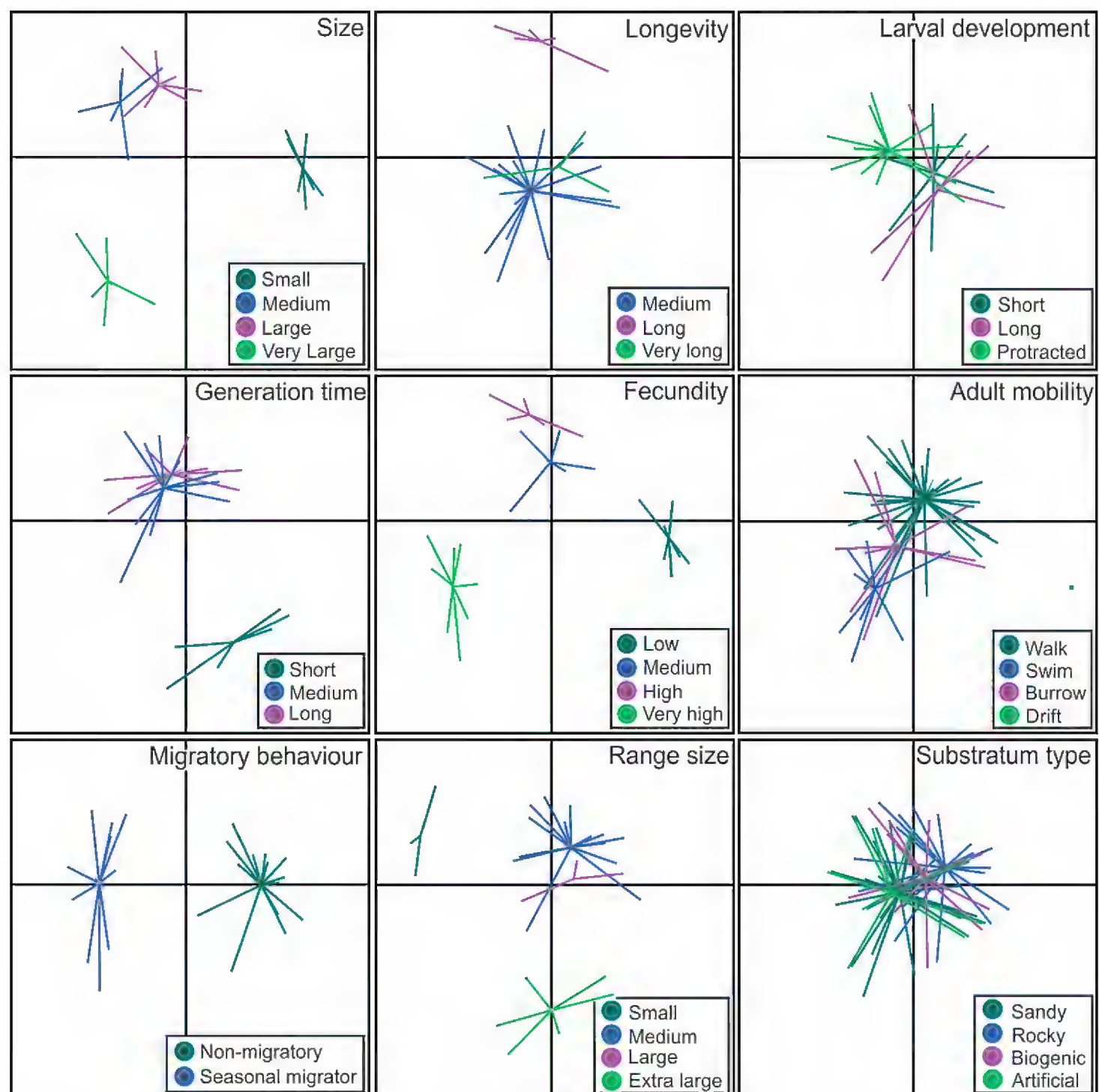


Figure 7. Fuzzy Correspondence Analysis bidimensional plot depicting the nine traits analysed. Each graph represents a single trait and the stars represent the categories within that trait.

not evident during the detailed trait analysis undertaken in this study and the mechanism behind the high number of Portunid invasions remains unclear. Despite 56 alien crabs being identified in this study, this number may be an under-representation of the true number of crab invasions, as records are not always genetically verified. This was the case in South Africa where *Carcinus maenas* was first reported (Le Roux et al. 1990), but a later genetic study highlighted the presence of the morphometrically similar sister taxa *Carcinus aestuarii* (Geller et al. 1997). The presence of such cryptic species may obscure the true prevalence of invasions (Marchini and Cardeccia 2017).

It has been suggested that species with large native ranges are likely to be successful invaders (Bates et al. 2013, Novoa et al. 2016). This is due to their tendency to have broad physiological tolerances ranges and generalist food and habitat requirements (Vazquez 2006, Troost 2010). This study, however, found no correlation between na-

Table 4. Correlation ratios per trait for the first two axes of the Fuzzy Correspondence Analysis (FCA). Traits highlighted in bold have highest correlation values for the respective axes.

Trait	Axis 1	Axis 2	Σ
Size	0.775	0.600	
Longevity	0.008	0.302	
Adult mobility	0.067	0.144	
Migratory behaviour	0.745	0.000	
Laval development	0.046	0.024	
Fecundity	0.716	0.414	
Generation time	0.073	0.428	
Range size	0.241	0.507	
Substratum type	0.050	0.017	
Variability explained (%)	16.23	14.55	30.78

tive and invaded range size. This outcome may be reflective of the coarse scale applied when defining range size. Due to the limited information available on the distribution of crabs, range size was unavoidably defined by the number of marine provinces from which a species had been reported. This is in contrast with the use of georeferenced records used in other studies that have detected a relationship between native and invaded range size (Hui et al. 2011, Bates et al. 2013). Nonetheless, such a relationship has been detected for some groups, even when the broad measure of latitudinal bands was used to quantify range size (Novoa et al. 2016). This may suggest that crab invasions are not truly characterised by a relationship between native and invaded range size or that, in the absence of genetic confirmation of taxonomic identity (both in their native and alien ranges) and baseline ecological surveys, it is not possible to detect such a pattern for crabs. Thus, while present data suggest no relationship between native and invaded range size for crabs, it is unclear if this is an artefact of the data used or a real reflection of the nature of these invasions.

The relationship between regions donating and receiving alien species can be complex, especially as receiving regions can themselves become donors (Grosholz and Ruiz 1995, Ruiz et al. 2000). As such, without genetic confirmation, the donor regions of most crab invasions remain unresolved. Nonetheless, by applying two different approaches, this study was able to identify some general relationships between donor and recipient regions of crab introductions. The first method, i.e. using native range as a proxy for donating region, is likely to be the more accurate for species with restricted native ranges. However, as native range size increases, so will the uncertainty associated with identification of donor regions. This problem was most evident in this study with respect to identifying the source of Mediterranean crab introductions. Many of these crabs have large native ranges spanning multiple bioregions, including the Arabian Seas, East Africa, North West Pacific, East Asian Seas and the South Pacific. Thus, despite the most parsimonious explanation being that these crabs invaded from the Arabian Seas via the Suez Canal (Galil et al. 2014), this method identified many bioregions as potential sources. In contrast, using shipping vector strength to identify donor

regions assumes that all introductions are related to the dominant vector of shipping. While this assumption may in fact be valid in many cases, when used on a species by species basis, this is likely to introduce significant error. Nevertheless, these methods identified two convergent patterns in predatory crab introductions. Firstly, the majority of alien crabs were found to be donated from the North West Pacific and secondly, the South Pacific received species from the most bioregions. The greater Western Central Pacific, which includes the North West Pacific bioregion, is one of the regions that supports the largest number of native crabs (Ng et al. 2008), suggesting that the large number of species originating from this region simply reflects high native diversity. This region is central in the shipping network (Seebens et al. 2013), suggesting high potential vector strength. As Brockerhoff and McLay (2011) highlighted shipping as the dominant vector of alien crabs and crab-like anomurans, it seems likely that high vector strength from this species-rich region accounts for the high number of alien crabs originating in the North West Pacific. The reason for the diverse sources of alien crabs recorded in the South Pacific remains unclear, but may reflect the diverse shipping network in the region.

Reflecting the highly invaded nature of the Mediterranean Sea (Galil 2009, Zenetos et al. 2012), this region was found to support the most crab invasions. While the well-studied nature of this region may contribute to the high number of recognised invasions, these elevated numbers are also likely explained by its central position in the shipping network (Seebens et al. 2013), its close proximity to many neighbouring regions and maybe most importantly, as a result of the Suez Canal (Katsanevakis et al. 2013, Galil et al. 2015). This canal offers a pathway from the Indo-West Pacific to the Mediterranean through which most crab species were introduced from the Arabian Seas. No Mediterranean species are found in the Arabian Seas as the sea water flow in the Suez canal is from the Red Sea to the Mediterranean Sea and not vice versa (Rilov and Galil 2009). The Australia and New Zealand bioregion is the second most invaded region, with more species known from New Zealand than Australia. However, as with the Mediterranean region, high search effort in both these countries may be reflected in this pattern. The absence of introductions to the Antarctic and the single introduction of Atlantic Rock Crab, *Cancer irroratus*, to the Arctic bioregion (Gíslason et al. 2014) mirrors the general pattern observed in marine alien species (Tavares and De Melo 2004) and is likely driven by the inhospitable nature of polar environments.

The role of traits in crab invasions

Traits suggested to be associated with successful invaders include longevity, large body size, high fecundity, long larval development, planktonic dispersal and broad environmental tolerance (Crawley 1989, Ehrlich 1989, Weis 2010, Hänfling et al. 2011). Despite specific traits having been identified as important for the invasion success of taxa such as cacti (Novoa et al. 2015), bivalves (Nawrot et al. 2015) and amphipods (Grabowski et al. 2007), this study found no patterns in the traits of alien crabs that

were associated with their invasion status or taxonomic identity (i.e. at the family level). This finding was unexpected and offered no support to the *a priori* hypotheses that (1) crabs with established populations would be characterised by traits allowing them to survive under a variety of conditions and (2) established and single record species would possess traits facilitating transfer by humans. Nonetheless, these results could be explained by several factors. Firstly, trait analysis requires the inclusion of as many species and traits as possible to provide the greatest resolution of important suites of traits (Bremner et al. 2006). While this study strove to address these requirements, limitations in the available literature resulted in nine traits being considered for 28 alien species. While this represents the first time that the traits of crabs have been assessed in such detail, the inclusion of more species and more traits in future analyses may result in the identification of important traits that were not detected in this study. Traits that have been suggested as important for invasion success, but which could not be included in this study due to the lack of information, included growth rate (Weis 2010), salinity tolerance (Hänfling et al. 2011), feeding activity (Spilmont et al. 2015) and larval dispersal potential (Brousseau and McSweeney 2016). Secondly, high levels of plasticity within traits enable species to adapt to a range of environmental conditions between and within the native and invaded habitats, thereby increasing their establishment success (Smith 2009). As such, the variability within traits and the plasticity with which they manifest might be key to invasion success. For example, *Eriocheir sinensis* and *C. maenas* show a significant increase in body size in their introduced region (Grosholz and Ruiz 2003). Similarly, alien populations of *Hemigrapsus sanguineus* show earlier sexual maturation (Brousseau and McSweeney 2016), while *E. sinensis* shows variability in sexual maturation rates when compared to native populations (Rudnick et al. 2005). Unfortunately, not all traits have been assessed in this detail and so this study was unable to consider variability in traits. An additional consideration relating to the assessment of traits relates to the theoretical approach applied. Ideally, studies should compare the traits of alien species with those that have never been recorded outside of their native ranges (Novoa et al. 2016). While the strength of such an approach lies in the fact that it contrasts information about species that have and have not spread outside their native range, this is also its greatest weakness as it is data demanding. Due to a paucity of knowledge on traits, even in native ranges, this approach is currently not viable for crabs. This lack of knowledge is notable, especially as crabs tend to be large, conspicuous and thus likely to be a well-studied group. Nonetheless, this approach may hold the key to identifying traits that are important for the invasion success of crabs in the future.

While some studies have highlighted traits that may be important in crab invasions, contrasting the findings of this study, it is important to consider the scale at which these were undertaken. These studies undertook single species comparisons, i.e. contrasted alien species between their native and invaded ranges (Grosholz and Ruiz 2003) or compared alien species with native species in a specific region (Brousseau and McSweeney 2016). While these studies are informative, it is important to acknowledge that their findings may be context dependent (Crawley 1989). The greatest strength of multi-species analyses, such as the one undertaken in this study, is that they are able

to elucidate general patterns present at a high taxonomic level. Nonetheless, they are limited by the availability of basic biological information and, while the limitations of the present study are acknowledged, this line of enquiry should be pursued when the underlying information becomes available.

Conclusion

The factors interacting to ultimately govern invasion success in crabs, as with marine alien species in general, are complex and it was not possible to identify traits predisposing species to being successful invaders with the data presently available. The application of trait-based analysis to answer this question does, however, hold promise. Presently, the greatest impediment to its extensive use in an invasion context is the lack of foundational biology knowledge for many taxa and an understanding of how basic biology varies geographically, i.e. across alien and native ranges. This could, however, be addressed by primary research aimed at developing a sound knowledge-base of species distribution and trait data. This would be most efficiently done through geographically broad collaborative projects, targeting groups that are already well studied. While many such groups are terrestrial, e.g. plants (Pysek et al. 2011) and birds (Blackburn et al. 2009), the collation of biological trait information for marine taxa has been receiving increasing attention (Costello et al. 2015). Most notable is the free access to trait data provided through the World Registry of Marine Species (<http://www.marinespecies.org>). It is thus suggested that coordinated research on well-studied taxa, such as intertidal mussels and barnacles, may offer a promising avenue for pursuing trait analysis as a methodology for advancing our understanding of invasion success in the marine context.

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Supplementary material I

List of 42 marine alien brachyuran crab species

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: List of 42 marine alien brachyuran crab species that were not considered in this study. Species are listed per family and the reason for the exclusion is indicated for each: P (Not a predator); D (Diet not defined); N (Native range not defined).

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Link: <https://doi.org/10.3897/neobiota.39.22002.suppl1>

Supplementary material 2

Sources used for reviewing crabs

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: Databases and publications used in the compilation of the list of predatory marine crabs and information on their distribution, vectors and traits.

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Supplementary material 3

Fuzzy coded trait data utilised in the FCA analysis

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: Fuzzy coded trait data utilised in the FCA analysis. Details are provided for established and single record species.

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Link: <https://doi.org/10.3897/neobiota.39.22002.suppl3>

Supplementary material 4

List of species assigned 'Single record' status

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: List of species assigned 'Single record' status and the reason for doing so. The references from which the information was sourced are also provided.

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Link: <https://doi.org/10.3897/neobiota.39.22002.suppl4>

Supplementary material 5

The native and recipient regions of the 56 alien crab species

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Explanation note: The native and recipient regions of the 56 alien crab species considered in this study. Regions were defined in terms of the 18 IUCN bioregions (Kelleher et al. 1995a, b, c, d).

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